

About earthworm communities in a rain forest and an adjacent pasture in Peru

by

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Abstract

Earthworms were collected from a primary forest and a four-year-old pasture near Panguana Biological Station (Dpto. Huánuco, Peru). The sites are located in the preandine zone of the Peruvian rain forest, where the forest is being increasingly replaced by pasture. It can be expected that the soil fauna changes accordingly. This is shown by the earthworm community. In the litter layer of the primary forest, mainly epigeic species of Glossoscolecidae of Neotropical distribution were found. In the pasture in contrast, the peregrine glossoscolecid, *Pontoscolex corethrurus*, is dominant, a species that inhabits the mineral layer of the soil. The total abundance of worms decreased in the pasture to about one half of that in the forest. These results are compared with data available from other rain forest, savanna and pasture sites.

Keywords: Earthworms, Amazonian soils, clearing effects, *Pontoscolex corethrurus*, Panguana, Peru.

Introduction

The Amazonian tropical rain forest is characterized by the highest species number of plants and animals of any terrestrial ecosystems and has evolved during millions of years. This fact seems even more astonishing in view of the impoverished soils that dominate the region. According to SIOLI (1983) this forest grows only on, not from the soil, i. e. the soil mainly serves as substratum for the mechanical fixing of the plants, and do hardly store or supply nutritive substances as do soils in temperate zones. In consequence, the existing minerals circulate in a nearly perfect cycle between plants, animals and microorganisms. Logically, the whole system is very sensible to perturbations (LAVELLE 1984).

As shown by FITTKAU (1975), soils in the preandine zone are richer in minerals. Recent weathering products from the Andes give the soils a higher fertility than in

Central Amazonia. The region at the Rio Pachitea (Departamento Huánuco, Peru) belongs to that zone. There, cattle-breeders use pastures up to several decades.

During a short visit of J. R. in the rainy season 1985 to the biological station Panguana at the Rio Yuyapichis, an affluent of the Rio Pachitea, it was possible to examine earthworm communities of primary forest and recently developed pasture in this region with the aim to get an insight in the consequences of land conversion for these important soil inhabitants.

Material and methods

1. Investigation site

1.1. General description

The biological station Panguana - founded in 1968 by Prof. Dr. H.-W. KOEPCKE and his wife Dr. M. KOEPCKE (VERHAAGH 1989) - is situated about 220 m a. s. l. at the left side of the Rio Yuyapichis (9° 37' S, 74° 56' W) in the eastern part of Peru (Departamento Huánuco) (Fig. 1).

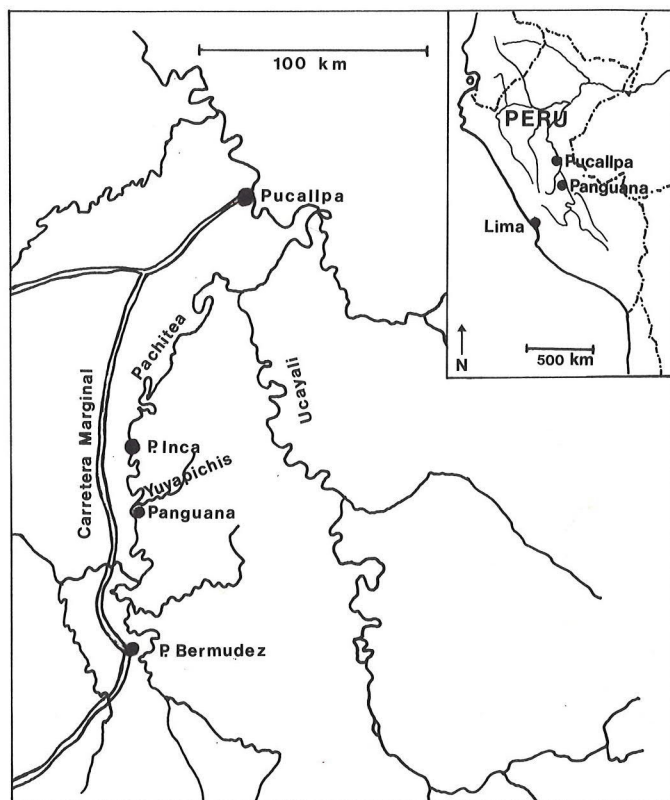


Fig. 1: Location of the biological station "Panguana" in Peru.

The region belongs in the Peruvian classification to the "zona del Rio Pachitea" (ONERN 1983) and is characterized as transition zone between the preandine slopes and the Amazon lowland. As the whole region the study area of Panguana is hilly, with the highest elevation at about 260 m a. s. l.

The vegetation type is classified as preandine hylaea (HUECK 1966); evergreen primary tropical rain forest (terra firme) and, to a small degree, different inundation vegetation (HANAGARTH 1981) are the natural vegetation. According to the classification of ELLENBERG (1959) and VARESCHI (1980) the forest of Panguana has to be considered as evergreen seasonal rain forest, because some trees loose their complete foliage during the dry season (SEIDENSCHWARZ 1986a, b).

The water level of the Rio Yuyapichis may oscillate several meters within days, but it never overflows the station or investigation sites.

Aside the natural ecosystems, there are different anthropogenic biotopes (pastures, plantations, and secondary forests in different stages of succession) near the station.

1.2. Climate

The existing data on the climate of Panguana cover periods of different length (4 - 7 years) during the years 1969 - 1985. Data quoted in this work (Fig. 2) are drawn from own measurements (M. V.) in 1983 - 1985 and from the following authors: HANAGARTH (1981), KOEPCKE in MEEDE (1984) and AICHINGER (1985).

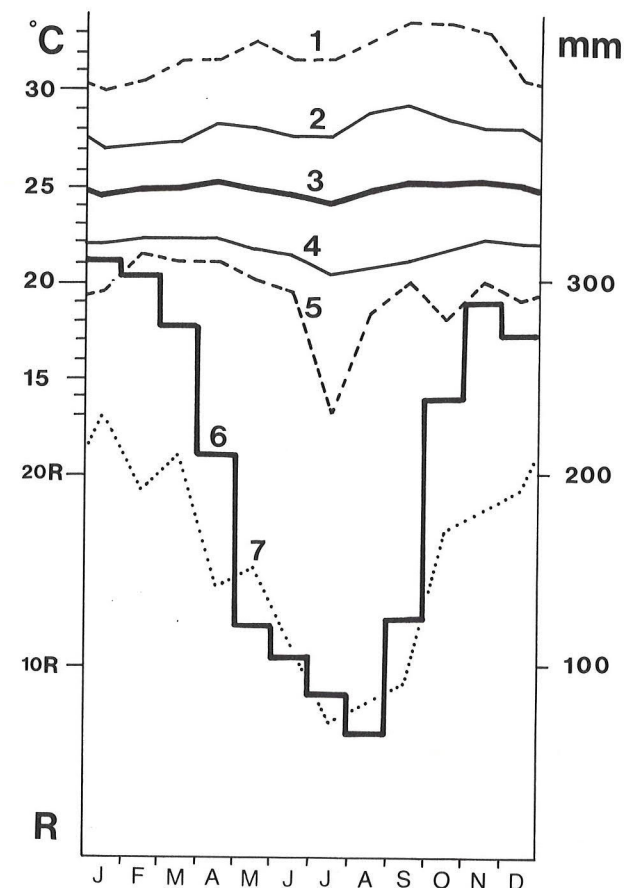


Fig. 2:

Climate of Panguana (values from 4 - 7 years): 1. - 5. temperature (°C). 1. absolute maxima; 2. average maxima; 3. mean temperature; 4. average minima; 5. absolute minima; 6. precipitation (mm); 7. rainy days (R).

General temperatures have to be considered as values of the forest border. Mean values are drawn from the average of the maxima and minima. Real mean temperature (e. g. by planimetry of temperature curves)

are therefore a little lower, because night minima last always longer than day maxima. The difference should be $\leq 0.5^\circ\text{C}$ (EIMERN & HÄCKEL 1984).

Mean annual temperature of the station is 24.8°C with a variance of $1 - 2^\circ\text{C}$, and should be in reality between $24 - 24.5^\circ\text{C}$. Mean maximal temperature is 27.9°C , mean minimal temperature 21.7°C . The difference of 20.5°C between absolute maximum (33.5°C) and minimum (13°C) is quite great, just as the maximal amplitude during some days in the dry season (up to 15°C). On the other hand, oscillation in temperature during the rainy season is very low.

Temperature of the forest interior averages 1°C below that of the station, and seldom passes 30°C in the understore. In the pastures maxima reach 40°C , and maybe even more at places with sparse vegetation (HANAGARTH 1981). At such locations temperature near the soil surface is higher than in upper strata. Mean temperature in the pasture is about 27°C . Soil temperature in general is about 24°C in the primary forest of Panguana and varies between 22 and 26°C , but reaches 28°C in prolonged dry periods (August). Differences between soil surface and 10 cm depth are minimal (Fig. 3b, c). In contrast soil temperatures in pastures are on an average about 4°C higher; soil surface temperatures extremely wave on sites with sparse vegetation (Fig. 3a).

With approx. 180 rainy days p. a. Panguana exhibits a pronounced rainy season from end of October to April with rain maxima in November and January (Fig. 2). It is followed by a significantly drier period of about 5 months duration with only 20 % of the whole annual precipitation. Annual rain fall sums up to 2403 mm showing variation between 1998 and 3007 mm.

There are but two months with a precipitation less than 100 mm (July: 85 mm, August: 65 mm). None of them has to be called arid in accordance with the concept of the minimum precipitation at 60 mm or the index of aridity of DE MARTONNE (LAUER 1952). If this could be verified by more data, the clima of Panguana would not be of the type Amw'i or Amw''i as normally considered to be true for the whole region (REINKE 1962), but of the type Afw''i: no month with a precipitation beneath 60 mm, winter dry, two rain maxima.

Relative air humidity in the lower strata of the forest averages nearly saturation during the day course, only in dry periods it drops to 60 - 70 % at midday. In the pastures oscillations are naturally stronger. Minima of 50 %, or even less on very windy days, are quite normal.

For more data on climate of Panguana, especially for different habitats, see HANAGARTH (1981).

1.3. Characterization of soils

Unfortunately, different classification systems for tropical soils still exist, and various names for the same soil type are in synonymous use. SEIDENSCHWARZ (1986a) uses the US soil system (SOIL SURVEY STAFF 1975; BOUL et al. 1980) to classify the soils of Panguana as Oxisols of the Umbriorthox group (Orthic and Rhodic Ferralsols in the FAO system (FAO 1973)). This estimation does not coincide with our own observations, and the classification of Peruvian officials who apparently conducted the only soil survey in the region up to now (ONERN 1983). According to that semi-detailed analysis the soils in the vicinity of the Pachitea valley consist of recent, subrecent and antique alluvial land on tertiary subsoil forming terraces at different levels.

The soils of our investigation sites belong to the "Cumapa" series, which is dominated by soils classified as Aquic Dystropept (orden Inceptisol, suborden Tropept) in the US system or as Dystric Cambisol in the FAO system. These soils show a low water permeability and an insufficient drainage. Therefore, they are mostly wet in the deeper layers (backwater), especially in the rainy season.

The "Cumapa" soils developed from subrecent fluvial deposits, show a low pH (4.5 - 5.5), high Al saturation (40 - 70 %), low contents of bases (saturation less than 40 % in the mineral layer) and mineral nutrients. Especially potassium is rare. Their natural fertility is classified as medium. Limiting factors for agriculture first of all are the poor drainage and their low or medium contents of mineral nutrients. Therefore, they are mainly used as pastures.

According to our observations, soils in the vicinity of Panguana are very inhomogenous due to different proportions of clay, and the often changing relief. Loamy, extremely wet sites with gleyic characters might be found not far from quickly drained sands with podzolic signs to mention the extremes. At extended sites

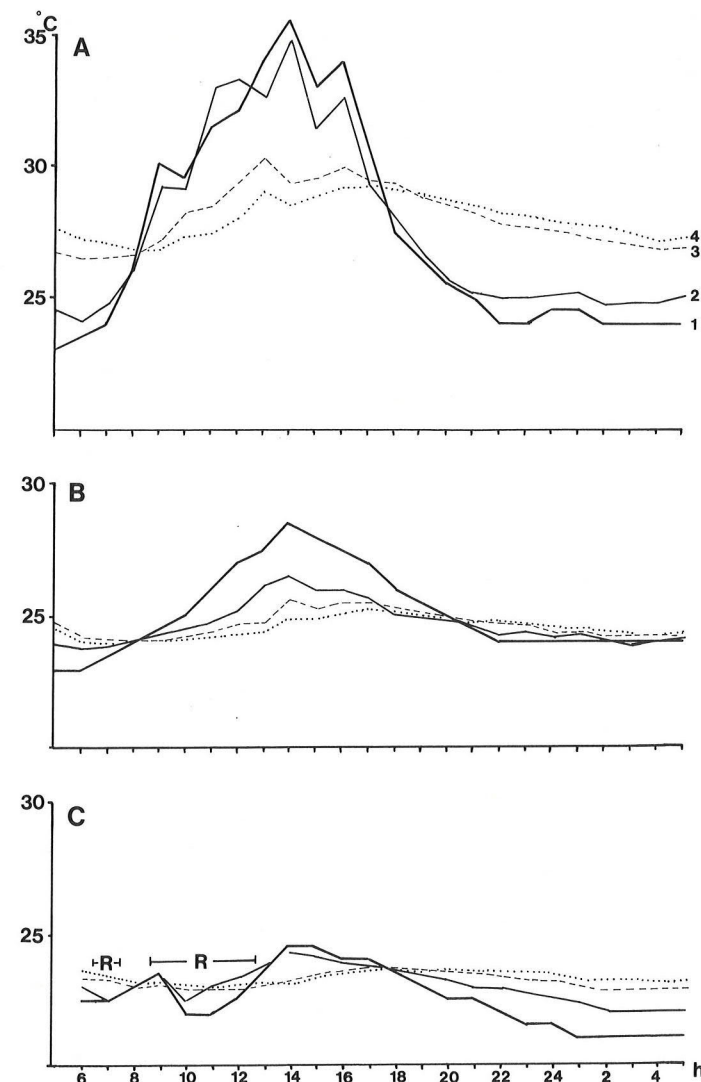


Fig. 3:

Examples of air and soil temperature during 24 hours in Panguana. A. Outside the forest, soil with sparse vegetation but shaded; sunny day during the rainy season (4.-5.1.1985). B. Primary forest; sunny day during the rainy season (4.-5.1.1985). C. Primary forest; rainy day at the end of the dry season (7.-8.10.1983). - 1. air, 2 m high; 2. soil surface; 3. soil, 5 cm depth; 4. soil, 10 cm depth; R = rain (air temperatures $\pm 0.5^\circ\text{C}$, soil temperatures $\pm 0.1^\circ\text{C}$).

in the forest flint stones lay at the soil surface. In part, this observations are reflected in the map prepared by ONERN (1983). It already indicates near Panguana six different soil series: Fluvisols in the lowest terrace, and Dystric Cambisols in the median and high terraces and the hills. The soil series differ mainly in age, relief, profundity, texture, permeability, drainage, pH, Al saturation and availability of mineral nutrients, i. e. natural fertility.

1.4. Description of investigation sites

The investigation site in the primary forest was selected by chance, and laid about 50 m remote from the forest border, in a place with rich underwood. The samples were taken from two places within a distance of 5 m. The soil was densely covered with litter, mainly from different *Ficus* species.

The uppermost layer of the soil profile (Fig. 4) was strongly felted litter (2 - 3 cm thick) on raw humus (2 cm thick). The latter contained a relatively high amount of paled quartz grains just as many fine roots. The mineral soil consisted of loose sandy loams and loamy sands. Therefore, this site is quite different from a "typical" central Amazonian forest (BECK 1971; FITTKAU & KLINGE 1973), where the organic layer is usually less than 1 cm thick, and litter does not cover the whole ground.

The pasture, about 4 years old, was located between the river (100 m apart) and the forest border (30 m apart). One of the two sample sites laid close to a depression with an oscillating water level during the investigation period. The whole area was densely covered by "Brakearia" grass (*Brachiaria ruzizensis* fide SEIDENSCHWARZ 1986a). Sporadically bunches of the herb "Mata-Pasto" (*Pseudelephantopus spiralis* (LESS.); Asteraceae) grew among the grass. This weed is common especially on elder pastures. Since the clearing of the area remnants of big trees slowly rot on the pasture ground.

The soil profile (Fig. 5) showed a dark coloured stratum (2 cm thick) consisting of roots, rotten plant parts, and humous material beneath the dense grass layer. After a very sharp black border (ash traces) followed the loamy-sandy subsoil.

Very high numbers of earthworm casts were found close to the station huts; thus, additional samples were taken there. In this area neither plants nor any organic layer could be found. The soil profile showed no horizontal differentiations in the uppermost 30 cm. The place has been cleared at least 20 years ago.

Table 1 shows the soil pH-values of the investigation sites. The measurements were conducted with the Hellige-Testsystem (Hellige Co., D-7400 Freiburg, FRG) and a pH-electrode (1 g soil in 2.5 ml Aqua dest.). Given values in Tab. 1 are the average of 3 (Hellige) or 2 measurements (electrode), respectively. The test solution of the Hellige-system records dissolved and bound H-ions, whereas the electrode in Aqua dest. just measures dissolved ions; therefore, the values of the Hellige-system are lower. In general, the soils show an acid reaction, the strongest at the forest site.

For the determination of the actual soil moisture (Table 2) three mixed samples from the uppermost 5 cm were taken and dried at 250 °C (moisture values are given in percent). Heavy rains were recorded between both sample dates: 84.4 mm (February) and 43.9 mm (May). The data shown in Table 2 depend mainly from the degree of ground cover: in the forest, where sun nearly never reaches the ground directly and the water capacity of the soil is relatively high due to the higher content of organic material, values are almost doubled in comparison to the pasture. In the vicinity of the station the moisture content of the barely grown soil reaches only 25 % of the amount at the forest site.

2. Extraxtion methods

During the investigation period February/March 1985 3 handsorting (QH) and 3 formalin (FO) samples were taken within two weeks on each sample site (in total 5 sites: both 2 in the forest and the pasture, and 1 near the station). Each sample represents 4 repetitions, each of 1/9 m². All worms were fixed in 70 % alcohol.

2.1. Hand-sorting

First, at all three sites (forest, pasture, station) soil samples (each of 1/9 m²) up to 40 cm depth were taken. In the forest no worms could be found beneath 5 cm; therefore, on all following sample dates only the organic litter layer was searched.

In the pasture, earthworms belonging to the same species as those caught in the root layer, were found very rarely in deeper layers. Only at the station site a significant number of the population lived in depths around 30 cm.



Fig. 4:
Soil profile in the primary forest.



Fig. 5:
Soil profile in the pasture.

Tab. 1: pH-values of soils in Panguana.

	Forest	Pasture	Station
Hellige	4.7	5.7	5.5
Electrode	5.6	6.6	5.8

Tab. 2: Actual soil moisture (%) in Panguana.

	Forest	Pasture	Station
Rainy season			
23.02.85	58.8	32.6	15.2
27.02.85	61.6	36.2	17.6
Dry season			
17.05.85	23.2	17.5	3.2
21.05.85	29.2	25.6	7.2

2.2. Formalin extraction

A 0.3 % Formalin solution was used to drive out worms from the mineral soil layers. This method is useful in the temperate zone, but often fails in the tropics (DASH & PATRA 1972). In Panguana it was most efficient at the station site. Despite many investigations, up to now it is not clear which parameters determine the results of the formalin extraction. Those worms in the forest and the pasture, which came into contact with formalin, showed very vehement movements. This behaviour facilitated their catch, but these specimens belonged always to the same species as those caught by hand-sorting (Epigees = litter inhabitants).

2.3. Biomass

The biomass was determined according to SATCHELL (1969). After short air-drying the fixed worms were weighed individually. After FRAGOSO (1985), the species *Pontoscolex corethrurus* loses 25 % of its weight when fixed in formol. SENAPATI & DASH (1980) found nearly the same losses measuring different Indian species. Our data were recalculated using not only this difference but also an average weight of the gut content. After this recalculation the data are comparable with those cited by PETERSEN & LUXTON (1982): Milligram fresh weight (FW) with empty gut per individuum. The dry weight can be estimated using a factor of 0.16 (PETERSEN & LUXTON 1982).

Results

The following earthworm species found in Panguana were identified or described up to now (RIGHI & RÖMBKE 1987), but there are some more resident species still undescribed:

Forest sites

Glossoscolecidae:

Glossodrilus sp.

Glossoscolex crucifer RIGHI & RÖMBKE, 1987

Martiodrilus ecuadoriensis (BENHAM, 1982)

Martiodrilus ecuadoriensis papillatus RIGHI & RÖMBKE, 1987

Martiodrilus sp.

Periscolex yuya RIGHI & RÖMBKE, 1987

Ocnodrilidae:

Quechua sp.

Octochaetidae:

Dichogaster affinis (MICHAELSEN, 1890)

Pasture and station sites

Glossoscolecidae:

Pontoscolex corethrurus (MÜLLER, 1857)

Octochaetidae:

Dichogaster affinis (MICHAELSEN, 1890)

Dichogaster modiglianii (ROSA, 1896)

Dichogaster saliens (BEDDARD, 1892)

Most of the endemic species found belong to the family Glossoscolecidae. A still unknown number of undescribed species will very probably belong to the Glossoscolecidae or, to a lesser degree, will be small Octochaetidae.

Accidentally, some specimens of a very big glossoscolecid species (called "Quica mama" by the inhabitants) were caught at the forest border. These animals, around 30 cm long, are not taken into consideration in the interpretation. Due to their low population density, they were not caught during the normal sampling program. In contrast to other places in South America, no European lumbricids, introduced by man and often more abundant than the endemic species, could be found in Panguana.

1. Abundance

In total 494 earthworms were caught during this investigation. All data were recalculated to individuals per 1 m². The results are summarized in Table 3a (each value represents 4 repetitions), and means are given according to the method used. Nearly all worms caught at the station and around 40 % of those found in the pasture belonged to the only peregrine glossoscolecid, *Pontoscolex corethrurus* (Tab. 3b), whose biology is well known in comparison to that of the species endemic to the Neotropics (see discussion). Only rarely *Dichogaster affinis* occurred in the forest samples, whereas *P. corethrurus* was never sampled at forest sites; not even close to the forest border, where some samples were taken outside the presented program. This is in agreement with results of LAVELLE et al. (1987) who found *P. corethrurus* generally absent from undisturbed ecosystems, or just immigrating from neighbouring disturbed areas in a limited way (FRAGOSO 1985, and unpubl. data cited in LAVELLE et al. 1987). AYRES & GUERRA (1981) prove its occurrence in Brazilian terra-firme forests as well.

The large oscillation of the data shown in Table 3a is expectable due to the absolute low number of samples. Nevertheless, it is clear that the population density of earthworms is higher in the forest than in the pasture, independent from the method used. The difference between hand-sorting and formalin extraction at the station site is due to the individuals of *P. corethrurus* living in deeper strata (Tab. 3b).

The relation between juvenile and adult worms (Tab. 4) shows, that in Panguana, as known from many other investigations all over the world (EDWARDS & LOFTY 1977), the juvenile worms are much more abundant than the adult ones. In the case of dominance of *P. corethrurus* (at the station and, partly, in the pasture) the proportion of the adult worms increases up to a relation of 1 : 4. Comparable values (1 : 5) were found in an Indian grassland (KRISHNAMOORTHY 1985), and in Mexican forests (FRAGOSO 1985: 3.1 % to 37 % adults, with a mean of 21 %). At the forest sites in

some samples even no adult worms were caught. Since nothing is known about the life cycles of the endemic species living there it is not clear whether this is a result of the low number of samples or an indication of a seasonal rhythm.

Tab. 3a: Abundance of earthworms (Ind./m²) (QH - Hand-sorting; FO - Formalin extraction).

	Forest 1	Forest 2	Pasture 1	Pasture 2	Station
QH 1	63	0	0	0	36
QH 2	12	144	63	18	88
QH 3	153	62	63	40	56
\bar{x} QH	76	69	42	19	60
\bar{x} of two sites	72		30		
FO 1	40	84	44	68	112
FO 2	12	132	48	24	140
FO 3	60	56	4	4	204
\bar{x} FO	37	91	32	32	152
\bar{x} of two sites	64		32		

Tab. 3b: Dominance part of *P. corethrurus* (in % of abundance: average of three data).

	Forest 1	Forest 2	Pasture 1	Pasture 2	Station
\bar{x} QH	0	0	45.2	52.6	95.0
\bar{x} of two sites	0		48.9		
\bar{x} FO	0	0	37.5	21.9	88.2
\bar{x} of two sites	0		29.7		

2. Biomass

The results of the biomass measurements are shown in Table 5a. Each value represents again 4 repetitions. All data are given as mg fresh weight per m². Because all other worms caught in the pasture and at the station - members of the genus *Dichogaster* - were very small, the dominance of *P. corethrurus* at these sites is even higher in terms of biomass than of abundance (Tab. 5b).

In this case, the low number of samples is even more problematical. Due to the big weight differences between small and large animals (3 mg to 1200 mg), the occurrence

of few adults can trigger significant changes in the biomass of the whole population.

Very surprising is the absolute amount of earthworm biomass at the station site. The fresh weight is more than 4 times higher than in the forest, in spite of high temperature fluctuations, barely grown ground, and low input of organic material at this site.

Discussion

1. Situation in Panguana

Clearing of rain forest and conversion to pastures in the vicinity of Panguana has a dramatic effect on the species composition of the soil fauna (HANAGARTH 1981, 1983; VERHAAGH, 1991). This is also true for the earthworm cenosis.

There are two tendencies: First, the abundance of earthworms seems to decrease considerably in comparison between forest and pasture. Second, the species spectrum of the community is altered, and therewith the spectrum of ecological categories, too.

The forest species caught are all epigeic and live in surface litter. Apparently, they cannot exist in the pasture, where abiotic conditions have been changed drastically in comparison to the former habitat. Small epigeics are also frequent in the pasture where they inhabit the rhizosphere. These are mainly members of the families Ocerodrilidae and Octochaetidae which are taxonomically very difficult, so that it is still unknown to what extent they can exist in the forest, too. Maybe, they are immigrants from the littoral zone. There are also some endogeic species, of which the most important is the peregrine glossoscolecoid *P. corethrurus*. This species is most abundant nearby the station with up to 204 individuals per m² surpassing the total number of earthworms even at the forest sites.

At first glance the fact seems surprising that the decrease of the earthworm community in the pasture is not reflected in the biomass. The bigger Glossoscolecidae (up to 2 g FW) that live in the forest surface litter are so quick and agile that they might escape especially from hand-sorting. But even regarding this methodological fault, a difference between the earthworm biomass in the forest and pasture is not certain.

The relative high biomass in the pasture is due to the endogeic species *P. corethrurus*. This species represents an ecological category that is totally missing in the forest samples, perhaps because of high oscillation in the water regime of the soil.

The change in the composition of the earthworm community has certainly several reasons: Lack of a litter surface, different food resources, drastical changes in soil temperature and humidity during day and night, hardening and high compaction of the upper soil strata still favored by grazing cattle (LAL 1987, 1988). Most forest species are stenoecic and not preadapted to these new conditions (LAVELLE 1984; LAVELLE et al. 1987).

But there might be also some positive effects for earthworms in the new habitat, like a higher pH, and possibly, a more regular water regime, including a more rapid drainage in the rainy season accompanied with a better air supply, and a lower evapotranspiration in the dry season in comparison to the forest. According to LAVELLE (1984), the last effects leads to the paradoxon that under equal rainfall forest soils might be physiologically drier (higher pF-values) than corresponding savanna soils during the dry season. RANZANI (1980), also records water deficiency in a variety of Amazonian soils at certain seasons.

Tab. 4: Distribution of age classes of the earthworms (QH - Hand-sorting; FO - Formalin extraction).

	Forest 1	Forest 2	Pasture 1	Pasture 2	Station
QH juv.	96.0 %	100 %	71.4 %	88.9 %	75.6 %
QH ad.	4.0 %	0 %	28.6 %	11.1 %	24.4 %
FO juv.	93.1 %	81.9 %	75.0 %	91.7 %	85.2 %
FO ad.	6.9 %	18.1 %	25.0 %	8.3 %	14.8 %

Tab. 5a: Biomass of the earthworms (mg FW/m²) (QH - Hand-sorting; FO - Formalin extraction).

	Forest 1	Forest 2	Pasture 1	Pasture 2	Station
QH1	2257	-	-	-	11224
QH2	24	528	571	122	10786
QH3	230	714	5670	9510	5999
\bar{x} QH	837	414	2080	3211	9336
\bar{x} of two sites	626		2645		
FO1	2391	454	3323	340	6322
FO2	2843	11948	3745	1039	11131
FO3	9571	1364	1302	116	13441
\bar{x} FO	4935	4589	2790	498	10298
\bar{x} of two sites	4762		1644		

Tab. 5b: Dominance part of *P. corethrurus* (in % of biomass: average of 3 data).

	Forest 1	Forest 2	Pasture 1	Pasture 2	Station
\bar{x} QH	0	0	88.7	73.1	99.5
\bar{x} of two sites	0		80.9		
\bar{x} FO	0	0	94.4	67.4	94.3
\bar{x} of two sites	0		80.9		

2. Comparison with other tropical sites

Tropical rain forests average a double net primary production and annual litter fall in comparison with forests in temperate zones though featuring a great variability in this aspect (BECK 1971; UNESCO 1978; ANDERSON & SWIFT 1983; LEE 1983 according to several authors). The higher organic input is often (not always!) more than compensated by a more rapid decomposition and mineralization of the organic matter. Litter turnover takes often less than a year, the litter standing crop being smaller than in temperate forests (UNESCO 1978; ANDERSON & SWIFT 1983; LEE 1983; LAVELLE 1984). Nevertheless, the amount of litter alone should not be a limiting factor for earthworms, even regarding that it often might be of poor nutritive value (KLINGE & RODRIGUEZ 1968; HOWARD-WILLIAMS 1974), and soluble organic substances and minerals are rapidly leached by rain (LAVELLE 1984). On the contrary, organic matter content of soils is within the same size class as in temperate forests (LEE 1983 after SCHLESINGER 1977; UNESCO 1978), but in part highly polymerized (humic acids) and hardly usable as energetic source for soil animals (LAVELLE 1984). Some authors conclude a positive correlation between earthworm abundance and the amount of litter as possible food resource (e. g. NEMETH & HERRERA 1982) while others do not (ANDERSEN et al. 1983). At this aspect we have to consider that exact food requirements of tropical earthworms in most cases still rest to be examined. At least for some rhizophagous species litter plays a subordinate role as energy source (ADIS & BOGEN 1982). Other tropical species are geophagous, detritivorous or fungivorous (MADGE 1969; SCHALLER 1973; DASH et al. 1979).

In tropical savannas and pastures litter input and soil organic matter are drastically reduced in comparison with tropical forests and temperate grasslands as well (LEE 1983; LAVELLE 1984),

Tables 6 - 8 show abundance and biomass of earthworm populations of some other lowland tropical rain forests (mountain and cloud rain forests have been omitted), and some tropical grasslands in comparison.

In total, nine investigations with comparable data on earthworms in tropical lowland rain forests are presented. The sites diverge in climate (mainly the amount of rain), soil properties, and vegetation type. Abundance and biomass do not show a clear trend: the spread reaches from 1 specimen/m² in Thailand to 132 specimens/m² in Mexico. Because of the very different size of the individuals a location with high abundance must not show a high biomass and vice versa (e. g. LAVELLE & KOHLMANN 1984). Earthworm abundance in Panguana fits in the size class of other Neotropical rain forests, but biomass is reduced (see methodical discussion). A part of the differences may be due to distinct methods, as well as to collecting during different seasons. Nevertheless, the presumption of LEE (1983) that tropical lowland rain forests generally exhibit low figures of earthworms seems to be incorrect.

Tropical grasslands show on an average significant higher earthworm populations than in forests (Tab. 9). Difference is especially high in comparison with natural savannas, meanwhile abundance and biomass strongly decline in young anthropogenic pastures. Similar values as in natural savannas are found in the two old man-made grasslands (50 - 100 years or even older). In both cases (Laguna Verde, Mexico and Watut 2, Papua New Guinea) *P. corethrurus* is the dominant species (LAVELLE et al. 1981; STANDEN 1988). Unfortunately, no comparable investigations on earthworm faunas from natural Neotropical savannas are published.

Tab. 6: Characterization of rain forest sites with investigations on earthworms.

Site, Land	Altitude (m)	Mean Annual Temperature (°C)	Mean Annual Rainfall (mm)	Soil Type
Sabah, Malaysia	10	26	3206	Weathered yellow loams
Sarawak, Malaysia B	130	27	5100	Regosol
Sarawak, Malaysia C	220	22	5100	Red-yellow Podzols
Sarawak, Malaysia D	500	22	5700	Podzols + Regosols
Chiangmai, Thailand	400	25	1450	Lateritic Soil
Bulolo, Papua New Guinea	700	?	1527	Tuff + Sandstone
Laguna Verde, Mexico	170	28	1500	Volcanic Vertisols
Bonampak, Mexico	200	24	2609	Rendzina
Chajul, Mexico	150	25	2964	Alluvial Soils
San Carlos, Venezuela	120	26	3521	Laterits + Podzols
Panguana, Peru	220	25	2403	Dystric Cambisol

Tab. 7: Earthworm populations in rain forests (QH - Hand-sorting; FO - Formalin extraction; FL - Flotation).

Site	Abundance (Ind./m ²)	Biomass (g FW/m ²)	Method	Reference
Sabah	3	0.6	QH	KITIZAWA 1971
Sarawak B	92	1.1	QH	COLLINS 1980
Sarawak C	37	0.7	QH	"
Sarawak D	72	0.7	QH	"
Chiangmai	1	0.1	QH	KITIZAWA 1971
Bulolo	2	2.4	FO	STANDEN 1988
Laguna Verde	132	9.8	QH, FL	LAVELLE et al. 1981
Bonampak	80	10.7	QH	LAVELLE & KOHLMANN 1984
Chajul	77	3.4	QH, FL	FRAGOSO 1985
Chajul	120	42.8	QH, FL	"
San Carlos	51	12.7	QH, FL	NEMETH 1981
Panguana	68	2.7	QH, FO	This study

The results are surprising in regard to the lower litter input in savannas, and the low content of organic matter in the soils (LEE 1983; LAVELLE 1984). The litter in savannas even usually burns in bush fires every year (LAVELLE 1983a), an event obviously harmful to earthworm population, too (STANDEN 1988). The explanation is that the cenosis in forest and savanna are quite different at the species and ecological

level: savannas are dominated by oligo- and mesohumic geophagous species in deeper strata, and polyhumic geophagous species in the rhizosphere, which use mostly soil humic reserves (LAVELLE 1983b). The forests are mainly colonized by epigeic, detritivorous species likely feeding on litter substances, fungi or roots, or by geophagous species living in the upper strata (NEMETH 1981; LAVELLE & KOHLMANN 1984; FRAGOSO 1985).

Tab. 8: Earthworm populations in tropical grasslands.

Site, Land	Abundance (Ind./m ²)	Biomass (g FW/m ²)	Reference
Lamto, Cote d'Ivoire; Savanna	230	49.0	LAVELLE 1978
Foro-Foro, Cote d'Ivoire; Savanna	460	22.3	LAVELLE 1983a
Lubumbashi, Zaire; Young grassland, formerly forest	13	0.6	GOFFINET 1975
Berhampur, India; Savanna	432	30.2	DASH & PATRA 1977
Burla, India; Savanna	255	56.0	SENAPATI 1980
Pasture, formerly savanna	174	41.0	"
Watut, New Guinea; Old grassland, formerly forest, last burning 2 months ago	7	1.4	STANDEN 1988
12 months ago	56	38.1	"
Laguna Verde, Mexico; Pasture, formerly forest	700	47.0	LAVELLE et al. 1981
Panguana, Peru; Pasture, 4 years old, formerly forest	31	2.1	This study

Tab. 9: Mean values of abundance and biomass in tropical lowland rain forests and tropical grasslands (data from Tab. 7 and 8; the recently burnt grassland of Watut, Papua New Guinea has been omitted).

	n	Ind./m ²	g FW/m ²
Rain forests	12	61	7.3
Grasslands, total	9	261	31.8
Natural grasslands	5	310	39.7
Anthropogenic grasslands, formerly forest, young (Lubumbashi, Panguana)	2	22	1.4
formerly forest, old (Watut, Laguna Verde)	2	378	42.6

If such a system totally changes in a short time - e. g. the forest is clear-cut - a dramatical alteration and reduction of the soil fauna will be the result (CRITCHLEY et al. 1979; PERFECT et al. 1980), and the new habitat will need a still unknown time to build up a quantitative similar earthworm population like in natural savannas. This explains the results of the pasture in Panguana and the "savanne de degradation" of Lubumbashi. Both sites are relative young and situated on former forest soils. The gap left by earthworm species adapted to forest soils is then easily filled by preadapted species like *P. corethrurus*.

This strictly geophagous species is classified as a mesohumic endogeic species (BAROIS & LAVELLE 1986), or between the polyhumic and mesohumic categories (LAVELLE et al. 1987). It is widespread in the Neotropics as in other tropical regions as well (AYRES & GUERRA 1981; LAVELLE et al. 1987; STANDEN 1988). The species probably originates from forests of the Guayanese plateau (RIGHI 1984) from where it has been spread by man. LAVELLE et al. (1987) summarize the probable reasons why *P. corethrurus* can rapidly colonize newly created habitats in the tropics:

The species can live in a great variety of soils with different physico-chemical characteristics: pH-values between 4.0 - 8.1, sandy or loamy texture with 4 - 41 % clay content, very low (0.2 %, KNÄPPER & PORTO 1979) to high organic matter content. The worms tolerate soil temperatures between 15 and 35 °C, but reproduces only at 23 - 27 °C. LAVELLE et al. (1987) consider the species to have a low tolerance to drought being full active solely at soil moisture values of about 35 % (close to pF 2.5). As the optimum for growth, survival and reproduction they measured 50 - 55 %. However, they used a loamy substrate (a vertisol with 35 % water content at pF 2.5, and 20 % at pF 4.2) in their experiments which seems not to be the mostly inhabited soil type by *P. corethrurus*. Because it is often found in sandy soils in which water content at pF 2.5 is far lower than in a vertisol the species at least can tolerate very low soil moisture values as indicated by VANUCCI (1953), AYRES & GUERRA (1981) and by our own results (up to 204 Ind./m² at the station in sandy soil with the lowest water content). Apparently, the worms migrate deeper into the soil (≈ 30 cm) under these conditions as already observed by FRAGOSO (1985). Normally, they are active in the upper 10 cm of the soil.

The demographic pattern of the species is typical of the r-type. The species can reproduce parthenogenetically (GATES 1973), production of cocoons is high (50 - 100 cocoons per adult and year depending on soil moisture), as well as the hatching rate of cocoons; the young grow rapidly (LAVELLE et al. 1987).

The most important trait, however, to colonize successfully disturbed areas seems to be the ability of *P. corethrurus* to use even low contents of soil organic matter very effectively. The humic acids are cracked by ingested soil microflora which shows a mutualistic relationship with the earthworms: the earthworms add large quantities of water and soluble polysaccharids (mucus) from their anterior gut cells to the ingested soil thus generating a neutral environment with a rich and easily assimilated energy source. In this manner activated the microflora becomes able to digest the complex organic polymeres (BAROIS & LAVELLE 1986). The system is so effective that during the gut transit of 2 - 4 hours up to 19 % of the soil organic matter is digested. By consuming large quantities of soil (3 - 6 g soil per g FW daily, LAVELLE 1983b) there is enough energy available to the worms for rapid growth and high fecundity.

This also explains the high number of individuals of this species at the station in Panguana where it is without competition by other species, and could build up a population since at least 20 years.

Still unknown is the reason why *P. corethrurus* is absent or rare at undisturbed forest sites. We do not coincide with LAVELLE et al. (1987) that it might be because of poor adaptation to drought. Their own experiments show that fecundity of adults and growth of immatures rapidly decline near water-saturation of the soil, meanwhile generation time increases. Therefore, a low tolerance for the often water saturated forest soils during the rainy season seems to be a more reasonable explanation, even supported by the finding of AYRES & GUERRA (1981) that *P. corethrurus* exhibits a relative low resistance to anoxic conditions: worms start to die after 6 hours.

The effect of the drastic change in earthworm communities both in species diversity and ecological amplitude on soil system function is difficult to guess. Ecologists estimate that the role of earthworms is neglectable as primary decomposers in tropical ecosystems (SCHALLER 1960, 1961; BECK 1971; FITTKAU & KLINGE 1973; ANDERSON & SWIFT 1983). At least this is true in comparison with temperate zones, or with respect to the role of termites in the tropics. Excluding macrofauna from litter in mesh litter bag experiments did not always result in a slower decomposition (BULLOCK & KHONG 1969), it even might be accelerated (ANDERSON & SWIFT 1983).

In comparison to temperate soils, anecic species (e. g. *Andiodrilus* sp. in San Carlos, Venezuela; NEMETH 1981; NEMETH & HERRERA 1982) which draw leaves from the surface to their deeper subterranean galleries and set their casts to the soil surface, are rarely found in tropical soils. Absence or scarcity of litter feeders results in a lack of clay-humus-complexes (BECK 1971), typical for many temperate soils.

Nevertheless, there is no doubt about the high importance of earthworm activity in tropical soils. First, it includes an improvement of the physical properties of the soil: a good soil texture with a favorable distribution of pores is important for optimal gas exchange, water conduction and water retention capacity (AINA 1984; LAVELLE 1984; LAL 1988). Thus earthworms prevent soils from compaction with all its negative consequences. LEE (1983) indicates that in many parts of the tropics soil formation through earthworm activity is recognizable, but the distribution of such soils may be locally very irregular. Further, the influence seems to be limited mainly to the upper soil strata: between 2.5 cm in Nigeria (NYE 1955) and 20 cm in the Ivory Coast (LAVELLE 1978). Our own results from Panguana confirm this observation. Soil formation is mainly due to casting activity on the soil surface by certain species. In forests the observed amounts range between 5 and 10 kg/m²·year (NYE 1955; KRISHNA-MOORTHY 1985), in natural savannas up to 28 kg/m²·year (LEE 1983). These figures are quite the same produced by Lumbricidae in temperate ecosystems. Other, geophagous, species, devour huge quantities of soil (5 - 36 times their own weight every day) to use the organic substances (humic acids). In the Lamto savannas the total amount of ingested soil was estimated at 800 to 1200 t dry soil/ha·year (LAVELLE 1978).

In this way, earthworms play an important role in the mineralization of the organic humic substances, apparently with the help of microorganisms that are stimulated in their guts to enhanced activity as was shown in *P. corethrurus* (BAROIS & LAVELLE 1986). Earthworms even regulate their feeding activity dependent on the amount of hydrosoluble organic matter thus indirectly controlling the mineralization rate (LAVELLE 1984). Additionally, their casts show higher bacterial activity than the surrounding soil, e. g. for

P. corethrurus it is 40 % higher. This level is stabilized at least 15 - 30 days (LAVELLE 1984). Consequently, earthworm activity influences population dynamic and distribution of soil microorganisms (DASH et al. 1979). TORQUEMADA & ASAKAWA (1981) could show that effects on microbial life are mainly dependent on the general existence of earthworms, less on their absolute abundance.

A last important trait of their feeding activity is the concentration of scarce nutritive substances in their excretions. Casts of tropical earthworms contain higher concentrations in organic C, N, available P and cations, especially Ca, than does the surrounding soil they are feeding on (LAVELLE 1984; LAL 1988 from several authors). For *P. corethrurus* could be demonstrated also a potential for free N fixation in the gut (LAVELLE et al. 1987).

Hence, earthworms support plant growth in several ways, and the introduction of geophagous species like *P. corethrurus*, which are adapted to the soil conditions of plantations and pastures, into tropical agricultural systems has already been proposed (LAVELLE 1984).

Zusammenfassung

Die in den letzten Jahren zunehmende Entwaldung und Ausbreitung von Weideland im präandinen Regenwaldgebiet von Peru führt gleichzeitig zu einer Änderung in der Zusammensetzung der Bodenfauna. Dies wird durch einen Vergleich der Regenwurmzönosen im primären Regenwald und auf Weideflächen in der Umgebung der biologischen Station Panguana (Dept. Huánuco, Peru) belegt.

In der Streuschicht des Regenwaldes lassen sich überwiegend epigäische, neotropische Glossoscolecidae nachweisen, während in den Weideböden der peregrine Glossoscolecide *Pontoscolex corethrurus* dominiert, der den Mineralboden bewohnt. Die Abundanz der Regenwürmer ist in den Weiden um etwa die Hälfte gegenüber dem Regenwald reduziert. Die Ergebnisse werden mit Daten von anderen Regenwäldern, Savannen und Weiden in den Tropen verglichen.

Resumen

La destrucción acelerada de los bosques preandinos (Selva Central) en el Perú y su transformación en pastizales es acompañada por un cambio en la composición de la fauna edáfica. Se examinó este efecto cerca de la estación biológica Panguana (Dept. Huánuco, Perú) comparando la cenosis de Lumbricidos en suelos de selva virgen y de pastos nuevos. En la capa de hojas en descomposición del suelo selvático se encuentran en su mayoría especies neotropicales epigeas de la familia Glossoscolecidae. En cambio prepondera en los pastos el Glossoscolecido peregrino *Pontoscolex corethrurus*, que vive en el estrato mineral. La frecuencia total de las lombrices de tierra en los pastos se disminuye aproximadamente a la mitad de la del bosque primario. Estos resultados se compara con datos de otros bosques lluviosos, sabanas y pastizales tropicales.

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